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RESEARCH ARTICLE ARAŞTIRMA MAKALESİ

Feeding ecology and reproductive biology of the orange-spotted toadfish *Torquigener hypselogeneion* (Bleeker, 1852) (Tetraodontidae) in the Taşucu Bay, Mediterranean Coast of Türkiye

Türkiye Akdeniz kıyısındaki Taşucu Körfezi'nde turuncu benekli balon balığı *Torquigener hypselogeneion*'un (Bleeker, 1852) (Tetraodontidae) beslenme ekolojisi ve üreme biyolojisi

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Abstract: This study examines the feeding ecology and reproductive biology of the invasive pufferfish *Torquigener hypselogeneion* along the Levantine coast of Türkiye. A total of 400 specimens were sampled (2018–2019), with a length-weight relationship of $W = 0.0198L^{3.0144}$ (r = 0.983). Stomach content analysis identified 24 prey groups, with crustaceans, gastropods, and bivalves being the most significant. *T. hypselogeneion* exhibits fully opportunistic feeding behavior. The reproductive period spans July to October, peaking in September (GSI values). Relative fecundity averaged 29046 ± 1525 eggs. During the field surveys, it was determined that *T. hypselogeneion* was one of the most abundant invasive fish species in the coastal ecosystem in the study area. These findings provide key bio-ecological insights into *T. hypselogeneion* in the eastern Mediterranean.

Keywords: Invasive fish, lessepsian fish, opportunistic feeding, reproductive aspects, Levantine Sea

Öz: Bu çalışmada, Levant kıyılarında yayılım gösteren istilacı balon balığı *Torquigener hypselogeneion*'un beslenme ekolojisi ve üreme biyolojisi incelenmiştir. 2018–2019 yılları arasında toplam 400 örnek alınmış olup, boy-ağırlık ilişkisi $W = 0.0198L^{3.0144}$ (r = 0.983) olarak hesaplanmıştır. Mide içeriği analizinde 24 farklı av grubu belirlenmiş, bunlar arasında kabuklular, gastropodlar ve bivalvler en önemli besin grupları olmuştur. *T. hypselogeneion* tamamen fırsatçı beslenme davranışı sergilemektedir. Üreme dönemi Temmuz ile Ekim ayları arasında belirlenmiş olup, GSI değerleri Eylül ayında en yüksek seviyeye ulaşmıştır. Ortalama göreceli fekondite 29046 ± 1525 yumurta olarak hesaplanmıştır. Saha gözlemleri sırasında, *T. hypselogeneion*'un çalışma alanında en bol bulunan istilacı balık türlerinden biri olduğu tespit edilmiştir. Bu bulgular, Doğu Akdeniz'de *T. hypselogeneion*'un biyo-ekolojik özelliklerine dair önemli veriler sunmaktadır.

Anahtar kelimeler: İstilacı balık, lesepsiyen balık, fırsatçı beslenme, üreme özellikleri, Levantin Denizi

INTRODUCTION

The Tetraodontidae family, known as pufferfishes, includes 193 valid species worldwide (Fricke et al., 2025; Froese and Pauly, 2025). Until now, ten puffer fish species have been reported from the Mediterranean. When taking into account their origins, it is seen that five are Indo-Pacific (*Lagocephalus sceleratus* (Gmelin, 1789); *Lagocephalus guentheri* Miranda Ribeiro, 1915; *Lagocephalus suezensis* Clark and Gohar, 1953; *Torquigener hypselogeneion* (Bleeker, 1852); *Tylerius spinosissimus* (Regan, 1908)), four of them tropical-Atlantic puffer fish (*Sphoeroides marmoratus* (Lowe, 1838); *Sphoeroides pachygaster* (Muller and Troschel, 1848); *Sphoeroides spengleri* (Bloch, 1785); *Ephippion guttiferum* (Bennett, 1831)) and one cosmopolitan puffer fish species *Lagocephalus lagocephalus* (Linnaeus, 1758) (Vacchi et al., 2007). Among the Non-Indigenous Species (NIS), especially the Lessepsian pufferfishes come to the forefront with their adverse effects in the Mediterranean. Furthermore, pufferfish pose a significant public health risk due to their content of Tetrodotoxin (TTX), one of the most potent neurotoxins known. All pufferfish species of Indo-Pacific origin established in the Mediterranean ecosystem are toxic, with *T. hypselogeneion* being recognized as the most poisonous among them (Köşker et al., 2018).

Genus *Torquigener* generally includes species that do not exceed 20 cm in length, and also among the puffer fishes *T. hypselogeneion* is the second smallest species after *T. spinosissimus* in the Mediterranean. This small demersal species is found in the sandy and sea grass habitats in the coastal zone, usually in the range of 0-75 m (Mutlu et al., 2021). *T. hypselogeneion* is a carnivorous species that primarily feeds on benthic invertebrates on sandy bottoms (Ulman et al., 2023). The native distribution of the *T.*

hypselogeneion is the Indo-Pacific region: South Africa, Mozambique, Tanzania, Madagascar, Australia, Indonesia, Japan and the Red Sea (Froese and Pauly, 2025; Ramadan and Elhalfawy, 2019). Besides, the first record for the Mediterranean was made by Golani (1987) from Israel. After eighteen years, it has expanded its distribution and reported from the Turkish coast (Bilecenoğlu, 2005) and chronologically in 2006 from Rhodes / Greece (Corsini-Foka et al., 2006), in 2014 from the Syrian coast (Sabour et al., 2014), in 2015 from the Aegean Sea (Skarvelis et al., 2015; Yapıcı and Türker, 2015), in 2016 from the Egyptian coast (Farrag et al., 2016) and in 2018 from the Libyan coast (Al-Mabruk et al., 2018).

Data on the bio-ecological characteristics of *T. hypselogeneion* for both natural distribution areas and the Mediterranean are quite scarce (Çek-Yalnız 2017; Ergüden et al., 2020; Chartosia et al., 2021; Ulman et al., 2023). While these studies provide valuable insights into specific population characteristics and the biology of the species, the limited sampling areas may not adequately represent the entire Mediterranean region. Additionally, the lack of research along the eastern Levantine coast of Türkiye underscores the importance of the present study.

The purpose of the study is to identify the feeding and reproduction characteristics of the invasive *T. hypselogeneion* in the eastern Mediterranean region. The study aimed to identify both the feeding groups and feeding behaviour in order to reveal potential dietary competition with native fish species in the region, as well as the reproductive strategy of the species in the study area.

MATERIALS AND METHODS

Study area, sampling and laboratory procedures

Between June 2018 and June 2019, a total of four hundred *T. hypselogeneion* specimens obtained monthly from local fishermen operating in the Taşucu region (36.312778 °N-33.883611 °E), which is located in the northeastern Levantine Sea, were examined (Figure 1). The samples were immediately preserved in the field by fixation in a 4% formaldehyde solution. After the field studies, the specimens were transferred to the laboratory, where their total length and weight were recorded with an accuracy of 0.1 cm and 0.01 g, respectively. The specimens were then dissected, and their sexes were identified through a macroscopic examination of the gonads. The weights of the gonads and livers of each individual were recorded using a digital scale. Additionally, the ovaries with vitellogenic eggs and the stomachs were removed and placed in small polyethene vials filled with 4% formaldehyde to estimate the species fecundity and for a detailed analysis of food preferences.

Figure 1. Sampling location of the *T. hypselogeneion* on the eastern Mediterranean Sea coast of Türkiye (the black square: Taşucu)

Length-weight relationship and condition factor

The length-weight relationship (LWR) was calculated using the exponential regression formula of Ricker (1975), and the condition factor (K) was calculated for all individuals using the formulae according to Gulland (1969).

$W = a \times L^b$

$K = W/L^b \times 100$

Where; W: total weight (g); L: total length (cm);

a: coefficient of proportionality; b: growth exponent

K: condition factor

Reproduction

According to King (2007), the gonadosomatic index (GSI) and hepatosomatic index (HSI) were monthly calculated. The ripe ovaries were used to calculate fecundity (F). A portion of the ovaries was weighed, and the oocytes were counted and then proportioned to the total gonad weight. Finally, the relationship between fecundity and total length was calculated.

$GSI = \text{gonad mass} \times 100 \times \text{body mass}^{-1}$

$HSI = \text{liver mass} \times 100 \times \text{body mass}^{-1}$

$F = \text{mass of ovaries} \times \text{mass of counted portion}^{-1} \times \text{number of oocytes in the portion}$

Feeding ecology

In studies on feeding ecology, samples were grouped seasonally. Here, December-January-February represents the winter season, March-April-May represents the spring, June-July-August represents the summer season and September-October-November represents the autumn season. To determine the diet characteristics of *T. hypselogeneion*, stomach contents were analyzed. Food items were identified as the lowest possible taxonomic category. The quantitative importance of prey differences in the diet was analyzed as; percentage frequency of occurrence (%F, the percentage of stomachs in which a specific item occurs with all stomachs containing food); percentage number (%N, each prey item as percentage of a total number of food items in the sample); percentage mass (%W, the wet mass of each prey item, as a percentage of the total weight of stomach contents). The index of relative importance (IRI and %IRI) was calculated using the combination of the three methods. Dietary analysis was done according to (Hyslop, 1980; Cortés, 1997).

IRI=(%W+%N)×%F

To characterize the feeding state, the vacuity index (%VI) the percentage ratio of the empty and nearly empty stomachs to the number of stomachs was used (Berg, 1979).

Statistical analysis

According to the data of the index of relative importance (IRI %), the Bray-Curtis similarity matrix was used to compare the seasons. The most abundant prey species causing differences between seasons were identified using similarity percentages (SIMPER). All multivariate analyses were carried out with the PRIMER 6.1.18© statistical package (Clarke and Warwick, 1994). Diet breadth was calculated using Levin's standardized index (*Bi*) (Hurlbert 1978); $B=1/(\sum_i^n = 1 pi^2)$ where '*B'* is the trophic niche breadth, and '*pi*' is the proportion of item '*i*' in the diet, '*n'* is the total number of items. A cumulative prey curve was used to determine whether an adequate number of stomachs had been examined to describe the diet (Tiralongo et al., 2018).

RESULTS

The sexes were determined by analysing four hundred specimens, as 208 males, 138 females, and 54 were immature. The length values of pooled samples ranged between 3.7 cm- 12.7 cm with 8.7±1.68 cm mean (Figure 2). The weight values ranged 0.85- 41.55 g with 14.98± 7.72 g mean. For males, calculated mean length and weight were 8.7±1.3 cm and 14.81± 6.9 g; for females 9.6±1.14 cm and 18.67±6.7 g. The length class of 9-9.5 cm (27%) was dominant, while the classes of 3.5-4 cm and 12-12.5 cm had the lowest (1% and 0.5%) (Figure 2). The length-weight relationship was calculated as $W=0.0198L^{3.0144}$ (r = 0.983) for all specimens, and an isometric growth was observed for both males and females (*b* = 3.0144) (Figure 3).

The condition factor that was calculated monthly had the highest value in December and March, while the lowest was in November. (Figure 4). The monthly variations of the gonadosomatic index (GSI) in males and females were given in Figure 4. The GSI increased steadily from March to September and reached its highest value, followed by a sharp decline. The lowest GSI values, below 0.5, were calculated from October to November. The reproductive period of *T. hypselogeneion* was determined for the study area to be from July to October, and reproductive activity peaked when water temperatures reached the highest levels. Additionally, in March, just before the gonads began to develop, the hepatosomatic index reached its highest value (7.19) (Figure 4).

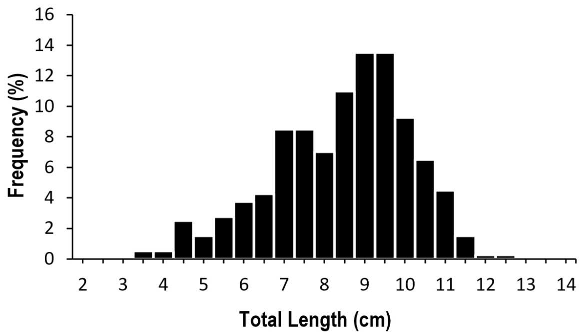

Figure 2. Total length-frequency distribution of all individuals of *T. hypselogeneion*

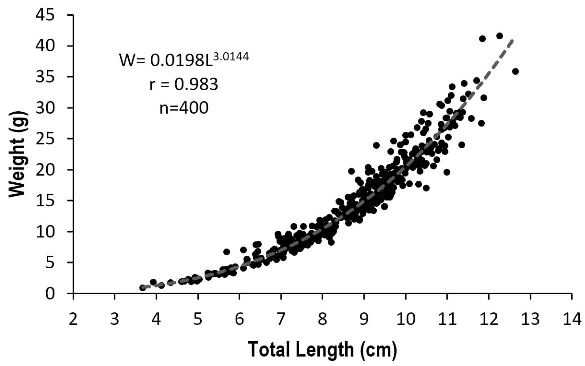

Figure 3. Length-weight relationship of all individuals of *T. hypselogeneion*

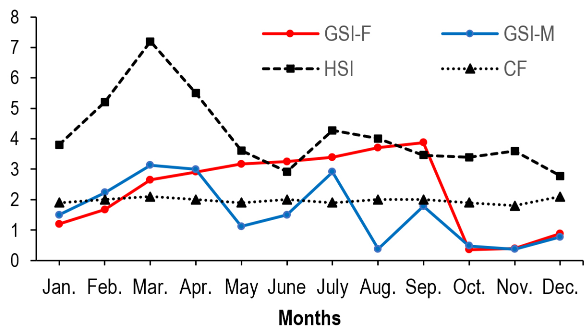

Figure 4. Montly condition factor (CF), hepatosomatic index (HSI) and gonadosomatic index (GSI-F: female; GSI-M: male) of *T. hypselogeneion*

The relative fecundity of *T. hypselogeneion* specimens (n: 31), varying between 8.7 cm and 12.3 cm in length, was calculated as a minimum of 12353, a maximum of 68400 and a mean of 29046±1525, and also the relationship between fecundity and length was very low (r=0.48) (Figure 5).

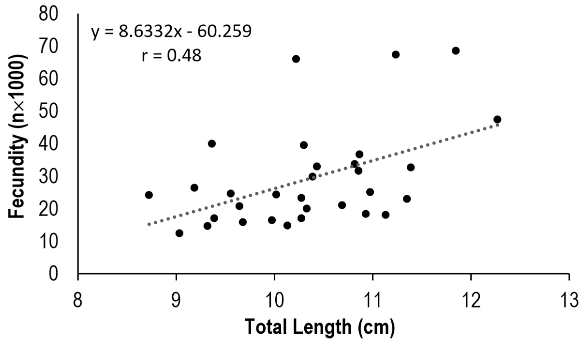

Figure 5. Total length-fecundity relationship of *T. hypselogeneion*

It was determined that 295 of the 400 stomachs examined were full, and 94 of them were empty (11 were damaged during dissection). The highest stomach fullness was 85.1% in summer, and the lowest was 60.9% in autumn (Figure 6). The high rate of stomach fullness in all seasons indicates that the fish do not have difficulty finding food.

A total of 24 different prey items were identified in stomachs (Table 1). According to % IRI, the most important prey group was the decapod crustaceans in all seasons (41.08% in winter, 64.7% in spring, 69.64% in summer and 53.05% in autumn) (Figure 7). In winter, ısopods (19.18%), Balanidae (9.24%) and gastropods (8.86%) were important prey items in the diet. In spring, unidentified pisces (14.17%), gastropods (5.31%), and polychaeta (4.72%) were important prey items. Those in summer included Trochidae, ranking second after decapod crustaceans at a rate of 9.84%. In autumn, unidentified pisces (31.46%) and bivalves (5.67%) were important prey items in the diet (Figure 7).

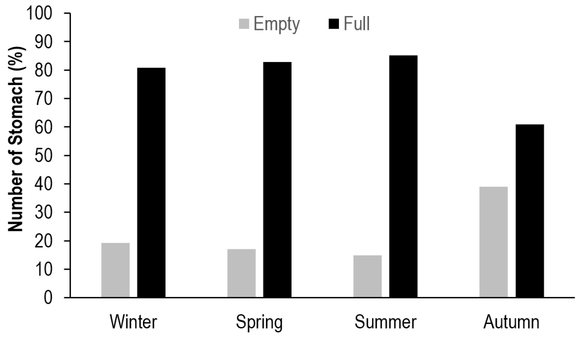

Figure 6. Seasonal vacuity index (VI) of *T. hypselogeneion*

Table 1. Prey list of *T. hypselogeneion* (%IRI: Relative importance index, %W: Percentage of total weight of stomach contents, %F: Frequency, %N: Percentage of total number of food items in the stomach content)

Prey taxa	WINTER				SPRING				SUMMER				AUTUMN			
	%F	%N	%W	%IRI	%F	%N	%W	%IRI	%F	%N	%W	%IRI	%F	%N	%W	%IRI
Foraminifera																
Amphistegina lobifera	-	-	-	-	50.00	2.86	0.12	2.36	44.44	1.07	0.18	0.86	7.69	18.22	0.88	1.75
Annelida																
Polychaeta	20.00	0.71	0.29	0.62	33.33	8.57	0.37	4.72	-	-	-	-	-	-	-	-
Crustacea																
Copepoda (Calanoid)	100.00	0.14	-	0.44	-	-	-	-	-	-	-	-	10.00	4.67	0.10	0.57
Amphipoda	25.00	3.42	0.94	3.34	100.00	1.43	0.62	3.24	-	-	-	-	-	-	-	-
Isopoda	5.75	74.36	34.38	19.18	-	-	-	-	-	-	-	-	-	-	-	-
Decapoda																
Brachyura	-	-	-	-	-	-	-	-	100.00	0.36	3.05	5.28	-	-	-	-
Galathea spp.	-	-	-	-	100.00	1.43	0.12	2.46	100.00	0.12	0.09	0.32	-	-	-	-
Upegebia spp.	10.00	1.42	0.47	0.58	-	-	-	-	-	-	-	-	-	-	-	-
Penaeidae	100.00	0.14	0.41	1.69	-	-	-	-	-	-	-	-	50.00	0.93	1.37	1.38
Unidentified Decapoda	100.00	0.85	5.27	18.78	34.78	32.86	25.96	32.36	55.00	9.54	49.46	50.26	87.50	3.74	10.29	14.65
Stomatopoda																
Squillidae	100.00	0.14	0.79	2.86	-	-	-	-	-	-	-	-	-	-	-	-
Cirripedia																
Balanidae	53.33	2.14	3.51	9.24	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified Crustacea	25.00	11.40	17.67	22.30	50.00	22.86	18.01	32.32	73.91	2.74	14.19	19.38	100.00	10.75	21.18	38.08
Mollusca																
Gastropoda																
Monodonta spp.	-	-	-	-	-	-	-	-	6.67	1.79	1.75	0.37	-	-	-	-
Rissoa spp.	21.43	1.99	1.61	2.37	7.14	20.00	2.48	2.54	-	-	-	-	3.64	25.70	2.65	1.23
Bittium spp.	-	-	-	-	-	-	-	-	20.00	0.60	0.45	0.32	-	-	-	-
Cyxlope neritia	-	-	-	-	-	-	-	-	100.00	0.24	0.27	0.79	-	-	-	-
Trochidae	-	-	-	-	-	-	-	-	6.90	81.17	10.92	9.84	-	-	-	-
Pteropoda																
Cymbulia peronii	-	-	-	-	-	-	-	-	-	-	-	-	50.00	0.93	0.88	1.08
Unidentified Pteropoda	-	-	-	-	-	-	-	-	-	-	-	-	33.33	1.40	0.20	0.64
Unidentified Gastropoda	42.86	1.99	4.74	8.86	100.00	2.86	0.50	5.31	100.00	0.48	1.53	3.10	17.24	13.55	3.44	3.49
Bivalvia	20.00	0.71	0.61	0.81	-	-	-	-	39.13	2.74	8.03	6.53	24.00	11.68	8.14	5.67
Cephalopoda	100.00	0.28	0.06	1.05	-	-	-	-	-	-	-	-	-	-	-	-
Echinodermata																
Unidentified Echinodermata	-	-	2.31	-	-	-	43.35	-	-	-	5.39	-	-	-	2.16	-
Pisces																
Unidentified pisces	100.00	0.28	2.28	7.88	80.00	7.14	4.47	14.70	100.00	0.24	1.66	2.94	94.44	8.41	19.51	31.46
Unidentified digested contents	-	-	24.66	-	-	-	3.98	-	-	-	3.05	-	-	-	29.22	-

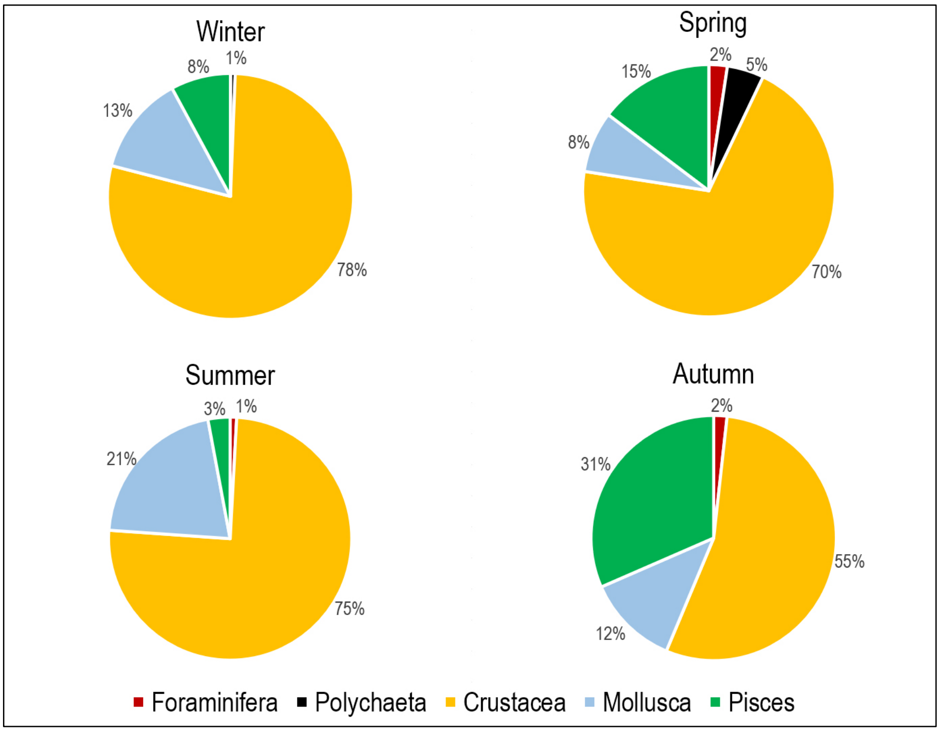

Figure 7. Seasonally stomach contents (main taxa) of *T. hypselogeneion*

The Bray-Curtis similarity analysis which is based on the %IRI results of the main prey groups, indicated that the winter season differed from the other three seasons (Figure 8). The results of the SIMPER analysis were listed in Table 2, and the prey items contributing the most to the differences in the winter season were determined as Isopoda and Cirriped crustaceans.

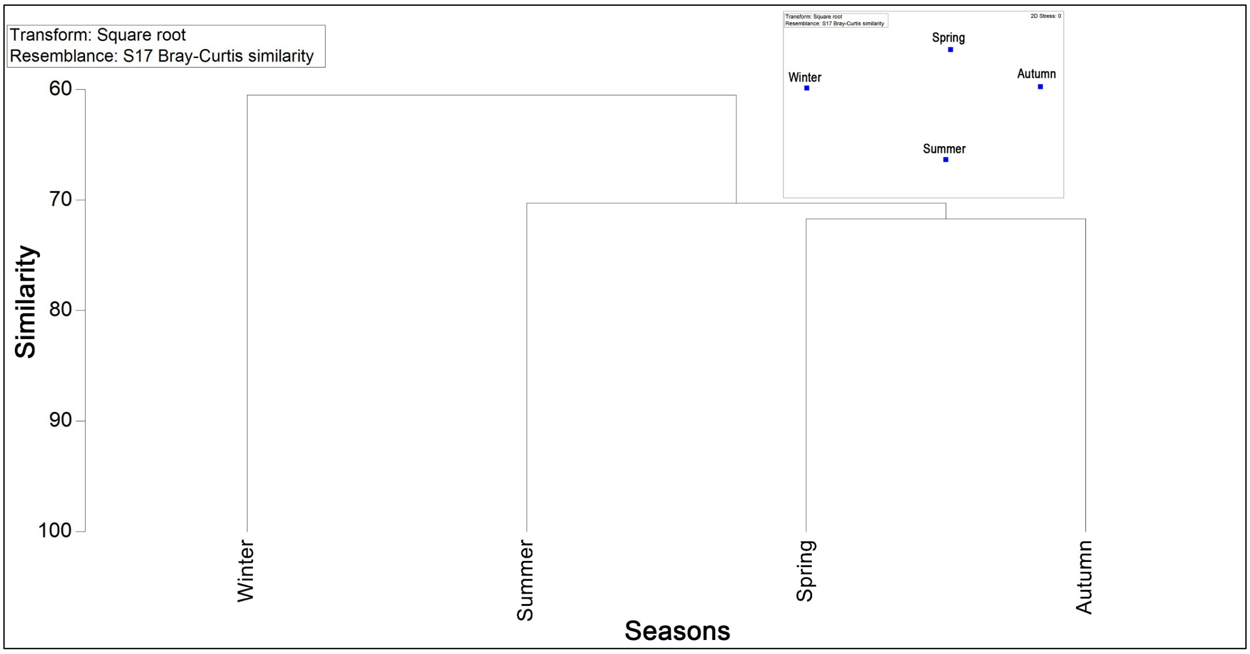

Figure 8. Similarity dendrogram based on cluster analysis and non-metric multidimensional scaling (nMDS) plot ordination of the main prey group (based on % IRI) between seasons

Table 2. SIMPER procedure to test the degree of dissimilarity (D) between seasons on the basis of the IRI% of the dominant main prey groups

Comparison between seasons	Prey taxa	Contribution to D (%)
Winter-Spring D=34.57	Isopoda	23.67
	Cirripedia	16.43
	Stomatopoda	9.14
	Foraminifera	8.30
	Polychaeta	7.49
	Decapoda	7.1
Winter-Summer D=40.95	Isopoda	21.12
	Cirripedia	14.66
	Decapoda	13.91
	Amphipoda	8.81
	Stomatopoda	8.15
	Bivalvia	7.98
Spring-Summer D=29.39	Bivalvia	19.5
	Polychaeta	16.57
	Pisces	16.17
	Amphipoda	13.73
	Decapoda	12
Winter-Autumn D=42.93	Isopoda	19.07
	Cirripedia	13.23
	Pisces	12.2
	Amphipoda	7.96
	Stomatopoda	7.36
	Bivalvia	6.45
	Unidentified	6.31
Spring-Autumn D=28.28	Bivalvia	17.74
	Polychaeta	16.19
	Decapoda	14.14
	Amphipoda	13.41
	Pisces	13.22
Summer-Autumn D=30.03	Pisces	29.07
	Decapoda	25.91
	Unidentified	13.2
	Gastropoda	12.13

Levin's standardized index calculations in our study indicated that the diet breadth value of the specimens was *Bi*= 0.37. Therefore, the species was identified as a specialist predator during all seasons (winter: *Bi*= 0.30; spring: *Bi*= 0.19; summer: *Bi*= 0.19; autumn: *Bi*= 0.22). The cumulative prey curve analysis results in this study indicated that the total sample size of this study was sufficient to describe the diet of *T. hypselogeneion* (Figure 9).

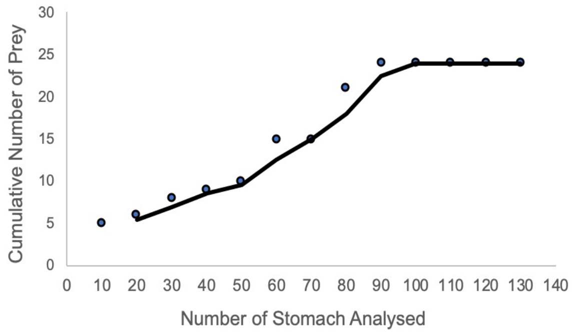

Figure 9. Cumulative prey curve as a function of sample size for fish with stomach contents analyzed in the diet of *T. hypselogeneion*

DISCUSSION

The first occurrence of *T. hypselogeneion* from Türkiye was reported by Bilecenoğlu (2005) and one specimen caught in September 2005 from the Göcek region in Fethiye (pers. obs. of the first author). Then, Irmak (2012) reported that this species is rare among other pufferfish in the Turkish coast only 3 specimens more than 100 trawl hauls in Taşucu region. On the other hand, the distribution and population of *T. hypselogeneion* increased after 2013 in the coasts of Türkiye (pers. obs. of the first author). During the field surveys, the angling experiments was conducted to test the density of *T. hypselogeneion* in the Taşucu region. In a 2-hour period, a total of 204 (34 non-baited and 170 baited) specimens were caught from 2 m depth from the inner harbour area with baited and unbaited sabiki rigs. Additionally, we want to express that we did not catch any native fish species during the angling experiments. Today, it has become one of the most widespread invasive species along the Levantine coast (Ulman et al.,2023). The Ministry of Agriculture and Forestry of the Republic of Türkiye supports pufferfish fishing as part of efforts to control pufferfish populations and provides a payment of 10 Turkish Liras (0.25 USD) per individual for this species, along with other Tetraodontids (Anonymous, 2025).

As one of the smallest members of its family, *T. hypselogeneion* has been reported to reach maximum total lengths of 18.5 cm (Golani, 1987), 11.6 cm (Ergüden et al., 2015), 12.1 cm (Çek-Yalnız et al., 2017), and 13.7 cm (Ergüden et al., 2020), 16.3 cm (Ulman et al., 2023) in various studies. Except the study of Golani (1987), other reports were compatible with our findings. According to the ' b ' value, the species have negative allometric growth in both sexes in many areas of the Mediterranean Sea (Ergüden et al., 2015; Bilge et al., 2019; Mutlu et al., 2021; Chartosia et al., 2021). Positive allometry in the species was only recorded by Ayas et al. (2019) from Mersin Bay. However, Ergüden et al. (2020) and Ulman et al. (2023) obtained results similar to our study (b = 3.0144), and they stated that the species have isometric growth. The variations in 'b' values may be attributed to differences in food availability and spatial-temporal factors among regions. Additionally, we believe that the distinct ontogenetic growth phases experienced by fish could also lead to different growth patterns.

Ramadan and Elhalfawy (2019) stated that the sex ratio was 1:1 and that the Red Sea populations of *T. hypselogeneion* reproduced during the summer period. In the present study, males were dominant, and the sex ratio was determined to be 1:1.5, with reproduction activity observed during the summer period (July to October). The differencies in the sex ratios may be due to sampling or spatial differences. GSI values in female specimens in the study began to rise in March and showed a sharp decline after September, but the same trend of gonad development was not observed in males in a few months, such as May and August. GSI values in these periods were far from indicating that the males were in the reproductive period. The possible explanation of the low GSI values of males could be related to either the small sample size of these months (i.e. in March, only five male specimens were sampled) or the smaller size of these fish when compared with other months (i.e. mostly below 9 cm). Because of that, when we take into account only female specimens, a similar reproduction period was observed with Ulman et al. (2023), who reported the spawning season as beginning in March for the populations of *T. hypselogeneion* in Fethiye and Cyprus coasts in the eastern Mediterranean Sea. The highest HSI values were observed in March, corresponding to the period just before the increase in GSI. In other words, fish utilize the energy stored in the liver for gonad development, which is reflected in the changes in HSI. Similar patterns have also been reported by Ulman et al. (2023) and Ramadan and Elhalfawy (2019). There is scarce data about the fecundity of *T. hypselogeneion*, and the mean relative fecundity in this study was determined to be 29046±1525. In contrast, Ulman et al. (2023) emphasized that *T. hypselogeneion* had an average of 1250 eggs per gram of fish weight in terms of fecundity. On the other hand, fecundity in the family Tetraodontidae is variable; for example, *Takifugu rubripes* has ~3 million, *Contusus richei* has 5000-100.000, and *Carinotetradon travancoricus* fecundity is only 279 (Habib, 1979; Kusakabe et al.,1962; Anupama et al., 2019).

The decapod crustaceans took the first place in the diet of *T. hypselogeneion* with a high rate in all seasons. Similarly, Chartosia et al. (2021) emphasized that decapod crustaceans were dominant in the diet of *T. hypselogeneion*. In contrast, Ulman et al. (2023) identified gastropods as the dominant prey group in the diet of *T. hypselogeneion* specimens from Fethiye, while emphasizing that decapod crustaceans remained the primary dietary component in specimens from Cyprus.

Additionally, the Copepoda, Isopoda, Amphipoda, *Upogebia* spp., *Galathea* spp., Squillidae and Balanidae taxa were also recorded in the diet. Gastropods were the most consumed prey in the Mollusca group. Moreover, feeding on sessile living organisms such as Balanidae and gastropods indicated that the species has an opportunistic feeding regime. Similarly, Krumme et al. (2007) emphasized that banded pufferfish are special predators feeding on *the Balanus* spp. *Amphistegina lobifera*, which has a high abundance and wide distribution in the coastal ecosystem, and is an exotic foraminifera for the Mediterranean, has been found in the diet of the *T. hypselogeneion* in the spring, summer and autumn. This exotic foraminifer species and Pteropoda have not been identified as prey items in previous feeding studies (Chartosia et al., 2021; Ulman et al., 2023). As a result, it was determined that *T. hypselogeneion* feeds on benthic invertebrates intensively. Despite the presence of fish in the diet of *T. hypselogeneion*, no fish sample that preserved its physical integrity was found in the stomachs. Instead, pieces of fish such as scales, vertebrae and fin rays were found. This showed that *T. hypselogeneion* fed on dead or injured fish, without direct predation. As a result, the jaw and tooth structure of the fish shred the feeding organism, making it difficult to recognize.

Although *T. hypselogeneion* was fed on many different preys, the main food consisted of crustaceans and gastropods. Furthermore, it was seen that it feeds on other preys that can be easily found in the benthos. Our findings and results of the Levin's standardized index revealed that *T. hypselogeneion* is an opportunistic invasive species and a specialist feeding behaviour. This trait indicates that it does not have difficulty finding food and likely constitutes one of the main reasons for the increasing distribution of *T. hypselogeneion* in the Mediterranean.

CONCLUSION

The favourable hydrographic conditions of the Levantine coast of the Mediterranean and its temperate seawater temperatures appear to provide suitable environmental conditions for the survival of this species. The results of the study indicate that the reproductive activity of the species peaks in September, when sea temperatures are at their highest. The findings also suggest that the Mediterranean coasts of Türkiye serve as a reproductive area for this species. Results of dietary analyses indicate that *T. hypselogeneion* is an opportunistic species that feeds on all types of benthic organisms available in its environment. Additionally, the identification of foraminifers and pteropods as prey items for the first time indicates a broader dietary spectrum than previously known. In particular, fishing harbors appear to act as attractive zones for this opportunistic feeder due to the availability of discarded fish and other marine organisms. This situation is believed to play a role in the increasing abundance of the species in the region. Efforts to support pufferfish fishing as part of control measures must be continued. In addition to this practice, fishing with traps can be encouraged in fishing ports where pufferfish populations are dense. It is necessary to conduct periodic monitoring of this species, which poses a threat to the ecosystem, socio-economic structures, and public health.

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AUTHORSHIP CONTRIBUTIONS

Erhan Irmak: Conseptualization, Supervision, Project administration, Investigation, Sampling. Uğur Özden: Investigation, Writing-Original Draft, Sampling and laboratory studies. Semih Engin: Supervision, Investigation. Adnan Çağlar Oruç: Writing-Original Draft, Writing-Review&Editing. Dilruba Seyhan Öztürk: Writing-Original Draft, Writing-Review&Editing. Sencer Akalın: Writing-Review&Editing.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

ETHICS APPROVAL

All applicable international, national, and institutional guidelines for the care and use of marine vertebrates were followed in this study.

DECLARATION OF AI USE

We have not used AI-assisted technologies in creating this article.

DATA AVAILABILITY

Data will be made available on request.

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